

# Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006

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The time-series of acoustically surveyed Antarctic krill (*Euphausia superba*) biomass near the South Shetland Islands (SSI) between 1996 and 2006 is re-estimated using a validated physics-based model of target strength (TS), and a species-discrimination algorithm based on the length-range of krill in plankton samples to identify krill acoustically, derived from TS-model predictions. The SSI area is surveyed each austral summer by the US Antarctic Marine Living Resources Program, and the acoustic data are used to examine trends in krill biomass and to assess the potential impact of fishing to the reproductive success of land-based predators (seals and penguins). The time-series of recomputed biomass densities varies greatly from that computed using an empirical log-linear TS-model and fixed-ranges of differences in volume–backscattering strengths ( $\Delta S_v$ ), conventionally used to identify krill acoustically. The new acoustic estimates of biomass are significantly correlated with both proportional recruitment and krill abundance estimated from zooplankton samples. Two distinct peaks in biomass (1996 and 2003) are in accord with recruitment events shown by net-based krill time-series. The foundation for the new TS-model and the associated krill-discrimination algorithm, coupled with the agreement between acoustic- and net-survey results, provides strong support for the use of the new analytical technique. Variable biases in the re-estimated krill biomass have been greatly reduced. However, survey variability increased as a result of the increased rejection of acoustic backscatter previously attributed to krill. Management of Southern Ocean krill stocks based on a precautionary approach may therefore result in decreased allocations of krill, given its dependence on the variability of survey estimates.

**Keywords:** acoustic survey, Antarctic krill, biomass densities, *Euphausia superba*, target identification, target strength.

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## Introduction

Antarctic krill (*Euphausia superba*) biomass in the Southern Ocean has long been estimated from acoustic data and a log-linear model of target strength (TS) against body length derived from empirical data (Greene *et al.*, 1991). This TS-model is coupled with a krill-identification algorithm based on the expected difference in volume–backscattering strengths at two frequencies ( $\Delta S_v : 2 \leq S_{v120\text{kHz}} - S_{v38\text{kHz}} \leq 12 \text{ dB}$ ; Madureira *et al.*, 1993). This approach has been used extensively on historical and contemporary data (e.g. Hewitt *et al.*, 2004a) to ascertain pre-exploitation biomass ( $B_0$ ) for input into fishery models (Hewitt and Linen Low, 2000; Hewitt *et al.*, 2002). The US Antarctic Marine Living Resources Program (AMLR) also used this technique to assess relative krill biomass in the South Shetland Islands (SSI) region during annual summer cruises (January–March) between 1992 and 2006 (Hewitt *et al.*, 2003).

Recently, Demer and his colleagues (Demer and Conti, 2003a, b; Conti *et al.*, 2005) developed an empirically validated, physics-based model of krill TS, building and expanding on the work by McGehee *et al.* (1998). This model, termed the stochastic distorted-wave Born approximation (SDWBA), includes the effect of body orientation and its variability, body length, mass, and other factors on the TS of krill (Conti and Demer, 2006).

Using the technique, Demer and Conti (2005) re-analysed the acoustic data collected during an international multi-ship, krill biomass survey of the Scotia Sea in 2000 (Hewitt *et al.*, 2004a). They demonstrated that the use of the SDWBA estimates for TS, holding all else equal, provided a substantially larger krill biomass than was estimated originally.

Because acoustically based biomass estimates are used to manage the international fishery on Antarctic krill, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) convened a panel of experts to review this new krill TS-model. The panel recommended that the SDWBA model be adopted by CCAMLR and further recommended that an enhanced krill-identification algorithm, based on SDWBA-predicted  $\Delta S_v$ , also be adopted (CCAMLR, 2005). The enhanced algorithm uses the range of krill body lengths in the sampled area to tune the SDWBA-predicted  $\Delta S_v$ , as opposed to the current practice of using a fixed range of  $\Delta S_v$  (i.e.  $2 \leq S_{v120\text{kHz}} - S_{v38\text{kHz}} \leq 16 \text{ dB}$ ) to identify portions of the echograms representing krill.

Time-series of net-tow data from the early 1980s until 2006 show fluctuations in krill abundance in the AMLR study site that are quasi-periodic, and that the patterns of recruitment are episodic and correlated with environmental conditions (Siegel

and Loeb, 1995; Loeb *et al.*, 1997). Similarly, time-series of acoustically estimated krill biomass, using the log-linear TS model (Greene *et al.*, 1991) coupled with the fixed- $\Delta S_v$  krill-discrimination algorithm, showed an 8-year cycle in productivity that broadly coincided with winter sea-ice conditions (Hewitt *et al.*, 2003), and exhibited similarities with an independent time-series from the northeastern Scotia Sea and significant correlations with other environmental conditions (Brierley *et al.*, 1999). However, despite the broad-scale accord, there was less accord between net- and acoustically-derived biomass, acoustic estimates showing increased biomass following periods of lower reproductive success (Hewitt *et al.*, 2003). As these time-series are used to manage the krill fishery, and to separate the effects of fishing and population variability of krill on reproductive success of land-based predators, it is important to resolve disagreements between the estimation methods, so that this Southern Ocean resource may be managed better.

Here, we examine how known biases in the acoustic estimates of krill biomass will be reduced by following CCAMLR's newly adopted protocols. The time-series of krill biomass in the SSI area estimated acoustically from 1996 to 2006 is therefore re-evaluated using the SDWBA TS-model and a krill length-dependent range of  $\Delta S_v$  (variable) for identifying krill. The new time-series is then correlated with net-estimated krill biomass and proportional recruitment. Finally, the results are discussed with respect to future challenges in the use of these new models, and in increased understanding of the dynamics of krill around the SSI, with the aim to improve the management of krill stocks in the Southern Ocean.

## Methods

AMLR has conducted a multidisciplinary survey (oceanographic, biological, and acoustic) in the SSI region, typically consisting of two sampling legs between January and March, each year since 1988 (Figure 1). Between 1988 and 1996, the survey focused on the area surrounding Elephant Island (the EI area). In 1997, the survey was expanded to include the north side of the SSI (the West area), and Bransfield Strait (the South area). These surveyed areas have ranged from 8102 to 43 865 km<sup>2</sup>. The current design (Figure 1) has been used since 2003, and usually includes at least five transect lines in each area (unless weather or ice impact the survey), from which acoustically based biomass and net-based abundance are estimated. Although most years have been represented by two surveys, sampling was limited to one survey (January) during 1997 and 2006 and (February) 2000. Some 100 stations are now occupied on each leg. The sampling techniques have been detailed extensively elsewhere (Lipsky, 2007).

### Sampling of krill

Krill samples collected from 1988 through 1993 were obtained using a 71-cm bongo frame fitted with 333- and 505-μm mesh nets. After 1993, sampling was conducted using a 6-ft (1.8 m<sup>2</sup>) Isaacs-Kidd midwater trawl (IKMT) fitted with a net of 505-μm mesh. Filtered volume was derived from a calibrated General Oceanics Flowmeter (Model 2030) mounted on the frame in front of the net. Nets were fished obliquely from a depth of 170 m, or to ~10 m from the seabed in shallower waters. Krill abundance is expressed as numbers per 1000 m<sup>3</sup> of water filtered. The West and South areas have been surveyed since 1997. A combination of net-based krill data from German

and AMLR surveys of the EI area (Siegel and Loeb, 1995; Loeb *et al.*, 1997) extends the temporal coverage in this region back to 1980. The German data are derived from rectangular midwater trawl (RMT 1 + 8, with nets of 300-μm and 4.5-mm mesh) samples.

Krill were removed from each sample and counted. All krill in samples with <100 individuals were measured for total length (TL; tip of rostrum to tip of telson). At least 100 individuals from larger samples were analysed in this way. Length frequency distributions and their ranges were developed for each area (EI, West, and South), for use in the acoustic estimates of biomass (Hewitt and Demer, 1993).

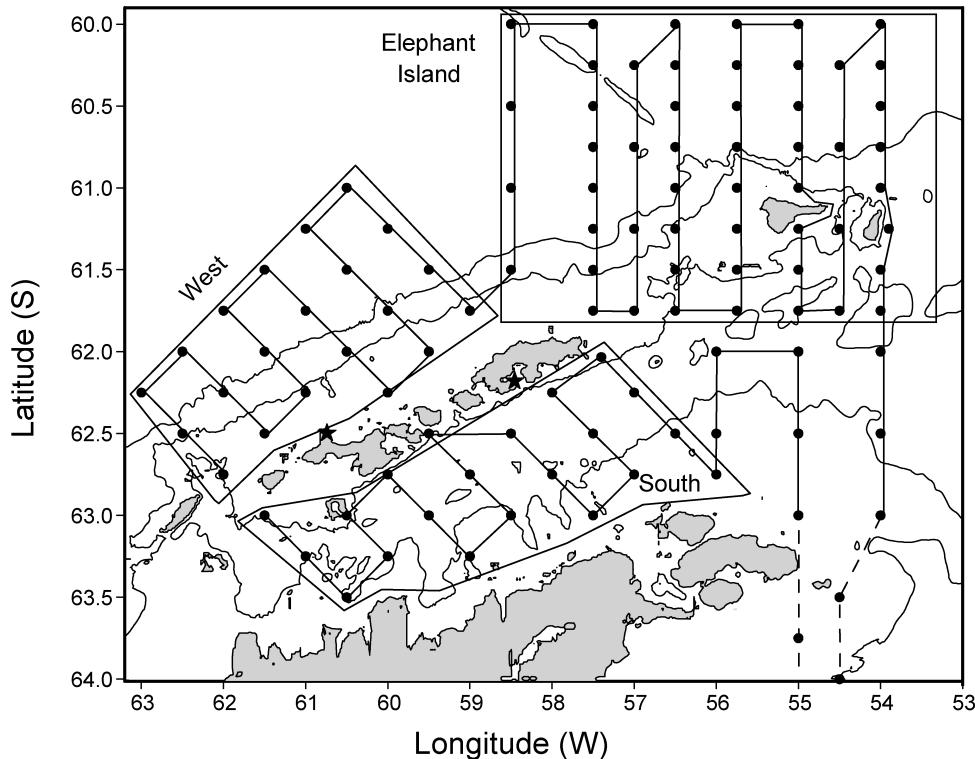
### Proportional krill recruitment

A time-series of proportional indices of krill recruitment has been developed for the EI area for the period 1980–2006 using the German and the AMLR net data by Siegel and Loeb (1995), Siegel *et al.* (1998), and Lipsky (2007). Proportional recruitment is defined as the ratio of the number of 1-year-old to the total number of krill. Length data were combined with numerical density data using CMIX (de la Mare, 1994a, b), a maximum likelihood-based algorithm that decomposes an overall-length distribution into age-specific distributions based on a mixture of normals. In cases where multiple surveys were available in a single year, the recruitment indices were combined by calculating the inverse, variance-weighted, mean proportional recruitment for that year (Siegel and Loeb, 1995).

### Acoustic estimation of krill biomass

The AMLR program uses multiple echosounders (four) operating at different frequencies (38, 70, 120, and 200 kHz), then relates volume-backscattering strengths ( $S_v$ ; dB re 1 m<sup>-1</sup>) at the different frequencies to apportion the integrated volume-backscattering coefficient (NASC; m<sup>2</sup> nautical mile<sup>-2</sup>) to krill and other co-habitant scatterers (see Hewitt *et al.*, 2003). NASC is then converted to numerical density using an estimate of krill TS (dB re 1 m<sup>2</sup>). The analytical method has evolved over the past two decades as the number of echosounder frequencies used has increased from 1 to 3. Before 1995, AMLR used a Simrad EK500 echosounder and one frequency (120 kHz), then two (120 and 200 kHz) frequencies initially deployed using a towed-body from, then hull-mounted on, the NOAA ship RV "Surveyor". From 1996 through 2004, the acoustic surveys were conducted from the RV "Yuzhmorgeologiya" with the EK500 configured for operating at 38, 120, and 200 kHz using hull-mounted transducers. In 2005 and 2006, surveys were conducted with Simrad EK60 echosounders and the same three frequencies. The current analysis is confined to the period 1996–2006, when data were collected at these three frequencies.

During all surveys, 1 kW pulses of duration 1 ms were transmitted at each frequency every 2 s. Geographic positions were logged synchronously, also every 2 s. The nominal vessel speed was 10 knots. System calibrations were conducted at the beginning and the end of each survey season using a tungsten-carbide sphere of diameter 38.1 mm, with 6% cobalt-binder material (Foote, 1990). Data used in the present analysis were obtained during transects between sampling stations. To minimize potential bias attributable to diel vertical migration of krill (Demer and Hewitt, 1995), only the acoustic data collected between local sunrise and sunset were used.



**Figure 1.** Current AMLR sampling grid (2003–2006) showing the locations of fixed stations (biological and hydrographic), and the general survey area. Polygons define the three US AMLR areas where biomass estimates are made. The 500 and 1000 m isobaths are displayed.

$S_v$ s at each frequency were averaged over 5-m depth bins and 100 s, background noise subtracted, and the  $S_v$  at 120 kHz ( $S_{v120\text{kHz}}$ ) was apportioned into regions of krill and non-krill using a multiple-frequency algorithm (see Hewitt *et al.*, 2003, 2004a, for details). The  $S_{v120\text{kHz}}$  attributed to krill was integrated from 15 m below the surface to either a maximum of 500 or  $\sim 5$  m above the seabed, resulting in NASC. Exceptions were in 1996, 1998, and 1999, when the maximum integration depth was 250 m (no significant differences were found; A. Cossio, unpublished data), but this should have a negligible effect because krill reside mostly in the upper 100 m (Demer, 2004).

### Species discrimination

The  $S_{v120\text{kHz}}$  was apportioned to krill or non-krill using two different algorithms: fixed- and variable- $\Delta S_v$  techniques. Both exploit the pairwise  $\Delta S_v$  at three frequencies (Demer *et al.*, 1999; Watkins and Brierley, 2002; Hewitt *et al.*, 2003) to discriminate krill from other co-habitant scatterers. The algorithms differ, however, on their assumptions about the frequency-dependence of sound-scattering from krill and the population dynamics of krill. In the fixed- $\Delta S_v$  technique, the same conditions are used to discriminate krill from non-krill targets regardless of the population dynamics. In other words, constant ranges of  $\Delta S_v$  are used to identify krill ( $4 \leq (S_{v,120} - S_{v,38}) \leq 16$  dB and  $-4 \leq (S_{v,200} - S_{v,120}) \leq 2$  dB). These ranges have been used by AMLR to estimate krill from the acoustic survey data collected since 1994. The variable- $\Delta S_v$  technique uses ranges of  $\Delta S_v$  based on the range of krill lengths found during each survey in multiple post-stratified areas. Guidelines for these minimum and maximum  $\Delta S_v$  values for different size ranges of krill were

determined using the SDWBA model of krill TS (Demer and Conti, 2003a, b; Conti and Demer, 2006), and tabulated to guide analyses (CCAMLR, 2005). Minimum and maximum  $\Delta S_v$  values used in this analysis are presented in Table 1.

### Models of TS

The NASC were converted to biomass density ( $\text{g m}^{-2}$ ) using two different TS models: the empirically derived log-linear model (Greene model; Greene *et al.*, 1991), and a simplified version of the SDWBA model (Conti and Demer, 2006). The simplified SDWBA model is an empirically validated, physics-based model of TS that includes variability attributable to krill size, shape, material properties, orientation, and acoustic wavelength. A normal distribution of orientations ( $\theta$ , the orientation angle) was used to derive the simplified SDWBA ( $\theta = N[\text{mean} = 11^\circ, \text{s.d.} = 4^\circ]$ ), estimated from the inversion of the SDWBA model using  $S_v$  measurements at multiple frequencies. Krill-/water-sound speed and krill-/water-density contrasts were fixed at 1.0279 and 1.0357, respectively. Both the Greene and simplified SDWBA models require distributions of krill TLs (length-pdfs) to derive weighted-mean, backscattering cross-sectional areas ( $\sigma$ ) on a per-animal basis ( $\sigma = 4\pi 10^{\text{TS}/10}; \text{m}^2 \text{ per krill}$ ; see Hewitt and Demer, 1993). Likewise, krill length-pdfs are also needed to calculate weighted-mean masses per animal ( $W$ ; g per krill) from an appropriate mass-to-length relationship. The latter relationship is based on net samples collected during the international survey of the Scotia Sea in 2000 (Hewitt *et al.*, 2004a):

$$W(\text{g}) = 2.236 \times 10^{-3} \times \text{TL}^{3.314}, \quad (1)$$

**Table 1.** Range of total lengths (TL, minimum–maximum) and acoustic  $\Delta S_v$ , ranges applied to assess biomass of Antarctic krill in the EI, South and West areas of the SSI region between 1996 and 2006, using the simplified SDWBA model (see Demer and Conti, 2003a, b; CCAMLR, 2005; Demer and Conti, 2005; Conti and Demer, 2006).

| Cruise | EI krill length (mm) | 120–38      | 200–120      | West krill length (mm) | 120–38      | 200–120      | South krill length (mm) | 120–38      | 200–120      |
|--------|----------------------|-------------|--------------|------------------------|-------------|--------------|-------------------------|-------------|--------------|
| 1996A  | 18–59                | 2.5 to 14.7 | −0.5 to 2.1  | x                      | x           | x            | x                       | x           | x            |
| 1996D  | 20–57                | 2.5 to 14.7 | −0.5 to 2.1  | x                      | x           | x            | x                       | x           | x            |
| 1997A  | 19–58                | 2.5 to 14.7 | −0.5 to 2.1  | 17–58                  | 2.5 to 17.7 | −0.5 to 6.8  | 15–52                   | 2.5 to 17.7 | −0.5 to 6.8  |
| 1998A  | 17–53                | 2.5 to 17.7 | −0.5 to 6.8  | 15–52                  | 2.5 to 17.7 | −0.5 to 6.8  | 16–44                   | 4.6 to 17.7 | −0.5 to 6.8  |
| 1998D  | 21–52                | 2.5 to 14.7 | −0.5 to 2.1  | 19–53                  | 2.5 to 14.7 | −0.5 to 2.1  | 19–48                   | 4.6 to 14.7 | −0.5 to 2.1  |
| 1999A  | 32–54                | 2.5 to 11.1 | −0.5 to 0.4  | 30–54                  | 2.5 to 11.1 | −0.5 to 0.4  | 26–52                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 1999D  | 35–56                | 2.5 to 11.1 | −0.5 to 0.4  | 36–51                  | 4.6 to 11.1 | −0.5 to 0.4  | x                       | x           | x            |
| 2000D  | 39–58                | 2.5 to 7.7  | −0.5 to −0.3 | 39–59                  | 2.5 to 7.7  | −0.5 to −0.3 | 40–55                   | 2.5 to 7.7  | −0.5 to −0.3 |
| 2001A  | 18–57                | 2.5 to 14.7 | −0.5 to 2.1  | 40–60                  | 2.5 to 7.7  | −0.5 to −0.3 | 22–55                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 2001D  | 26–60                | 2.5 to 14.7 | −0.5 to 2.1  | 26–60                  | 2.5 to 14.7 | −0.5 to 2.1  | 28–57                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 2002A  | 17–59                | 2.5 to 17.7 | −0.5 to 6.8  | 18–60                  | 2.5 to 17.7 | −0.5 to 6.8  | 20–45                   | 4.6 to 14.7 | −0.5 to 2.1  |
| 2002D  | 21–59                | 2.5 to 14.7 | −0.5 to 2.1  | 20–56                  | 2.5 to 14.7 | −0.5 to 2.1  | 20–49                   | 4.6 to 14.7 | −0.5 to 2.1  |
| 2003A  | 13–53                | 2.5 to 17.7 | −0.5 to 6.8  | 13–54                  | 2.5 to 17.7 | −0.5 to 6.8  | 13–45                   | 4.6 to 17.7 | −0.5 to 6.8  |
| 2003D  | 15–53                | 2.5 to 17.7 | −0.5 to 6.8  | 19–54                  | 2.5 to 14.7 | −0.5 to 2.1  | 16–49                   | 4.6 to 17.7 | −0.5 to 6.8  |
| 2004A  | 21–55                | 2.5 to 14.7 | −0.5 to 2.1  | 24–57                  | 2.5 to 14.7 | −0.5 to 2.1  | 20–57                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 2004D  | 29–58                | 2.5 to 11.1 | −0.5 to 0.4  | 22–55                  | 2.5 to 14.7 | −0.5 to 2.1  | 18–56                   | 2.5 to 17.7 | −0.5 to 6.8  |
| 2005A  | 20–59                | 2.5 to 14.7 | −0.5 to 2.1  | 21–57                  | 2.5 to 14.7 | −0.5 to 2.1  | 20–57                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 2005D  | 28–57                | 2.5 to 14.7 | −0.5 to 2.1  | 39–55                  | 2.5 to 7.7  | −0.5 to −0.3 | 19–53                   | 2.5 to 14.7 | −0.5 to 2.1  |
| 2006A  | 25–61                | 2.5 to 14.7 | −0.5 to 2.1  | 41–60                  | 2.5 to 7.7  | −0.5 to −0.3 | 26–59                   | 2.5 to 14.7 | −0.5 to 2.1  |

In 1996, data were not collected in the West and South areas (x).

and represents a fatter krill than previously used (Hewitt and Demer, 1993). Dividing NASC by  $\sigma$  yields the number density ( $\rho$ ;  $N$  nautical mile $^{-2}$ ), and multiplying  $\rho$  by  $W$  yields the biomass density ( $b$ ; g m $^{-2}$ ). Noting that the Greene model and mass relationships are both near-cubic functions of krill TL, Hewitt and Demer (1993) combined the two steps to generate conversion factors (CF) using a single length-pdf [ $CF = \sum f_i \times W(TL_i)/\sigma(TL_i)$ ; where  $f_i$  is the frequency of occurrence vs. TL]. However, because the simplified SDWBA predicts a TS that is highly non-linear and non-monotonic against length, the weighted-mean  $\sigma$  and  $W$  were each calculated before combining into a CF for each TS model, area, and survey (i.e.  $CF = \sum f_i \times W(TL_i)/\sum f_i \times \sigma(TL_i)$ ). The differences between the two methods are negligible when using the Greene model, but can be appreciable when using the SDWBA, especially if the length-pdfs are narrow.

## Biomass calculation

Finally, krill biomass (B) in kilotonnes (kt) was estimated by multiplying biomass density by the relevant area ( $A$ ; nautical mile $^2$ ). Details of these calculations and those for estimating sampling variance (CV; %) are documented extensively (Jolly and Hampton, 1990; Hewitt and Demer, 1993; Hewitt *et al.*, 2003, 2004a; Demer, 2004). Total biomass was estimated in three different ways for each area, survey, and year, using Method 1 (fixed- $\Delta S_v$  technique and Greene model), Method 2 (fixed- $\Delta S_v$  technique and simplified SDWBA model), and Method 3 (variable- $\Delta S_v$  technique and simplified SDWBA model). Always, the sampling variances were estimated. The data are presented in the Appendix.

## Results

### Krill length distributions

The length-pdfs of krill collected in the EI area between 1988 and 2006 show large proportions of small (<25 mm) krill, coupled with other modes of larger krill (Figure 2), indicating significant recruitment events in 1989, 1992, 1996, and 2002. In the 4 or 5 years following each event, the growth of individual krill in that cohort is visible as an increasing mean length of the associated modes, even as cohort biomass declines.

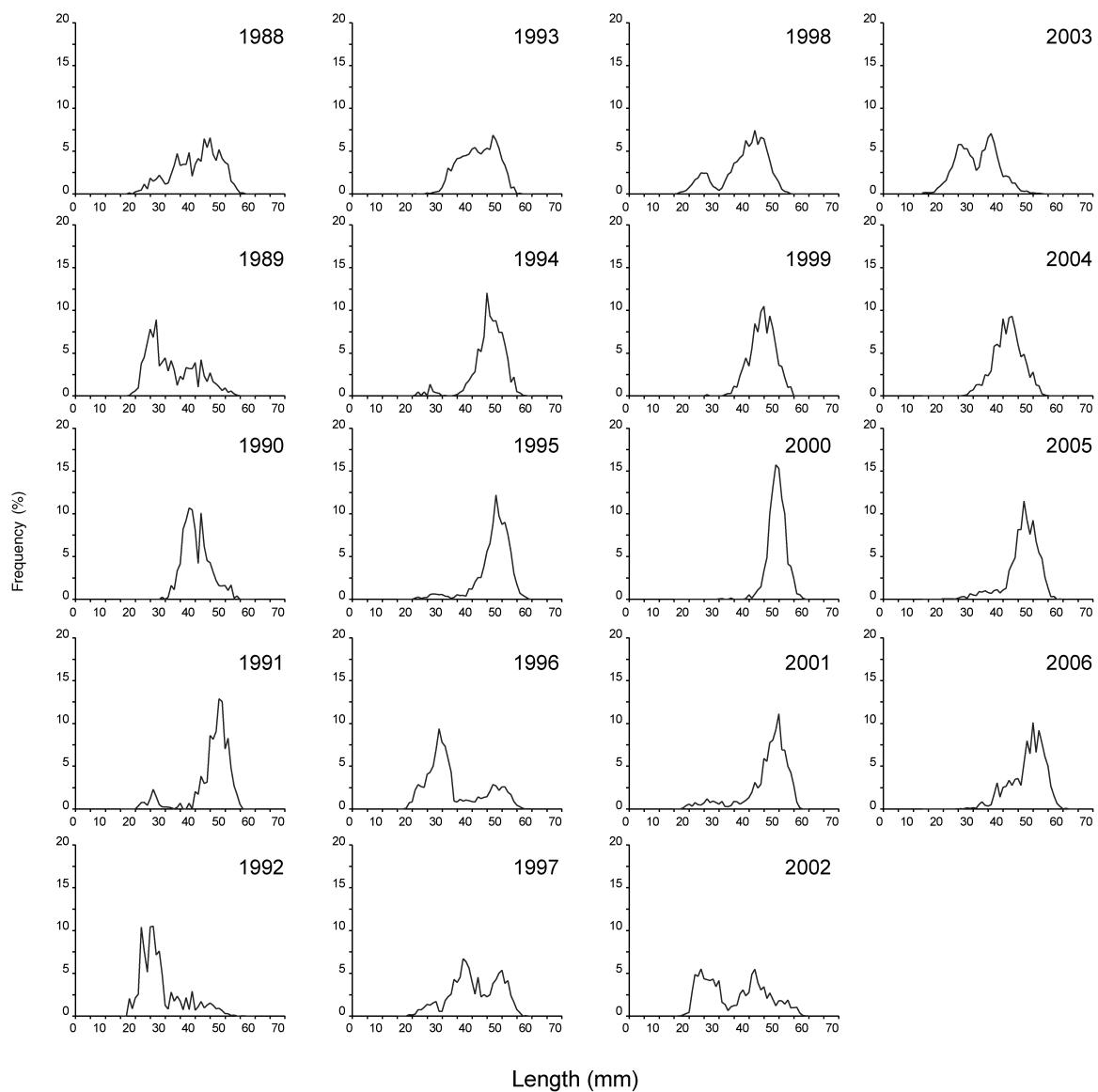
### Net estimated krill densities and proportional recruitment

Krill densities estimated from net samples in the EI area varied greatly between 1980 and 2006 (Figure 3a). Mean density was greatest ( $>400$  1000 m $^{-3}$ ) in 1982, and subsequent to that peak, the greatest densities were in 1996, 1998, and 2003, with 107, 94, and 203 krill 1000 m $^{-3}$ , respectively. Since 2003, krill densities have declined as the 2002 cohort has grown older (Figure 2).

Proportional recruitment in the EI area also varied greatly over the 26 years of data collection (Figure 3b). After the three strong recruitments in the 1980s, large recruitments were observed only during 1988/1989, 1995/1996, and 2000/2001 through 2002/2003 year classes. Over the past decade (1996–2006), proportional recruitment is significantly correlated with krill density ( $r = 0.53$ ,  $p < 0.02$ ), reflecting the importance of young animals to population abundance.

### Comparisons of krill biomass estimated acoustically

The time-series of acoustically estimated total biomass from 1996 to 2006 was estimated using Methods 1, 2, and 3, each as defined in the subsection biomass calculation, above. To simplify



**Figure 2.** Krill length distributions in the AMLR survey area between 1988 and 2006. Age/length cohorts are visible as modes progressing from  $\sim 25$  through 55 mm at periods of roughly 4 years. No significant cohorts are apparent over the last three field seasons.

visualization of the general patterns in the biomass trends, simple averages of annual estimates are used (Figure 4). Estimates of the CVs of each survey are given in the Appendix, and can be used to resolve point estimates of variability.

#### Method 1

Over the period analysed, total biomass in the EI area ranged from 3 million tonnes (Mt) in 2005 to  $<0.2$  Mt in 1993 (Figure 4a). Highest values of total biomass were in 1996, 1998, and from 2003 to 2005. Although there was good correlation among areas, the West and South areas had lower biomasses. Total biomass was not correlated with the net estimated krill density ( $p > 0.2$ ) or the proportional recruitment ( $p > 0.8$ ).

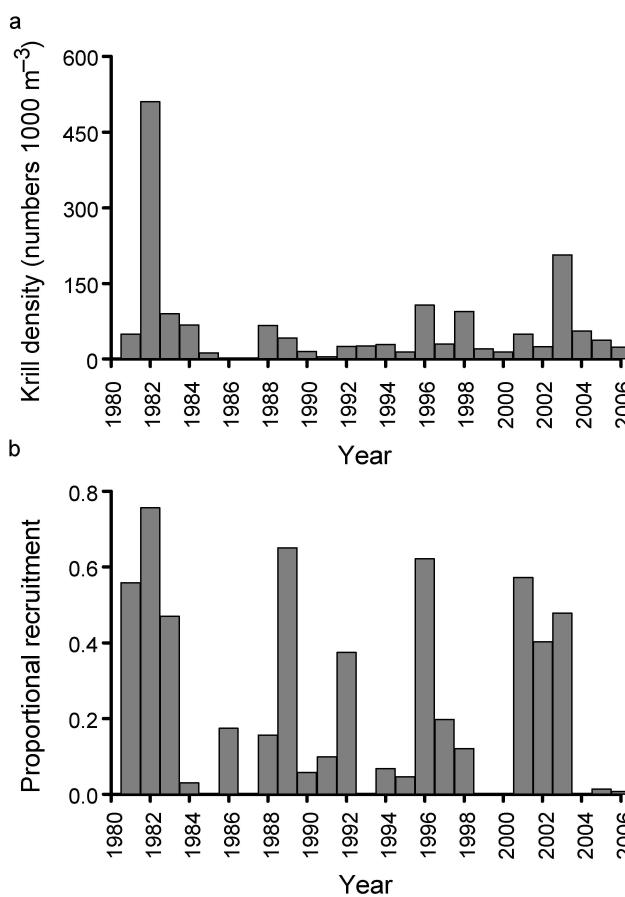
#### Method 2

Variations in the time-series of total biomass estimated using Method 2 are similar to those produced by Method 1, with

maxima and minima during similar periods (Figure 4b). Indeed, the two series are highly correlated ( $r > 0.95$ ,  $p < 0.0001$ ; Figure 5a). However, the values of total biomass estimated with Method 2 are roughly twice those estimated with Method 1. The CVs were exactly correlated between Methods 1 and 2 (not shown), indicating that, all else equal, the TS model simply scales the biomass within a stratum. Again, the total biomass estimated using Method 2 was not correlated with the net estimated krill density or the proportional recruitment.

#### Method 3

An entirely different time-series of total biomass is estimated (Figure 4c) when the variable- $\Delta S_v$  values (Table 1) are used to identify krill. Peaks in 1996 and between 2001 and 2003 are both followed by smooth declines. Total biomass was correlated between the EI, West, and South areas (all  $r > 0.89$ ,  $p < 0.005$ ). Also, the total biomass estimated using Method 3 is much lower



**Figure 3.** Time-series of (a) density, and (b) proportional recruitment of krill in the EI survey area between 1980 and 2006. Krill density was based on 71-cm bongo net samples from 1980 to 1992, and 1.8 m<sup>2</sup> IKMT samples from 1993 to 2006. Proportional recruitment reflects the proportion of 1-year-old krill as a function of the total krill abundance each field season. High proportional recruitment reflects favourable spawning seasonality, high reproductive output, and larval survival from the previous year (Siegel and Loeb, 1995).

than that estimated using Method 2, but close to that estimated using Method 1.

### Comparison of the output from the three methods

The time-series of total biomass estimated by Methods 2 and 3 are weakly correlated ( $r = 0.33, p < 0.02$ ) across all areas (Figure 5b). In contrast, their CVs were better correlated ( $r = 0.5, p < 0.001$ ), with a single outlier (Figure 5c). Not surprisingly, the CVs of the total biomass estimated with Method 3 had greater initial variability (intercept  $\sim 20.3\%$ ) than those estimated using Method 2. This results from the inherent patchiness of krill; greater variability along transects is created by eliminating more acoustic backscatter that is not “krill-like”.

The estimates of density from net tows and proportional recruitment are uncorrelated with the total biomass estimated using Methods 1 and 2, but significantly correlated with those estimated using Method 3 (Figure 6a). Correlations between net-estimated densities and acoustically estimated total biomass using Method 3 ( $B_3$ ) in the EI and West areas were significant ( $p < 0.025$ ), and  $r$  was 0.8 and 0.95, respectively. Correlations

between the total biomass estimated using Method 3 and proportional recruitment varied (Figure 6b) across these two areas, although the patterns were similar. In the West area, the relationship was not significant owing to periods of high proportional recruitment during periods of low biomass (2001 and 2002). The correlation between  $B_3$  and proportional recruitment in the EI area was high ( $r > 0.87$ ) and significant ( $p < 0.005$ ), yet the same 2 years also affected the correlation.

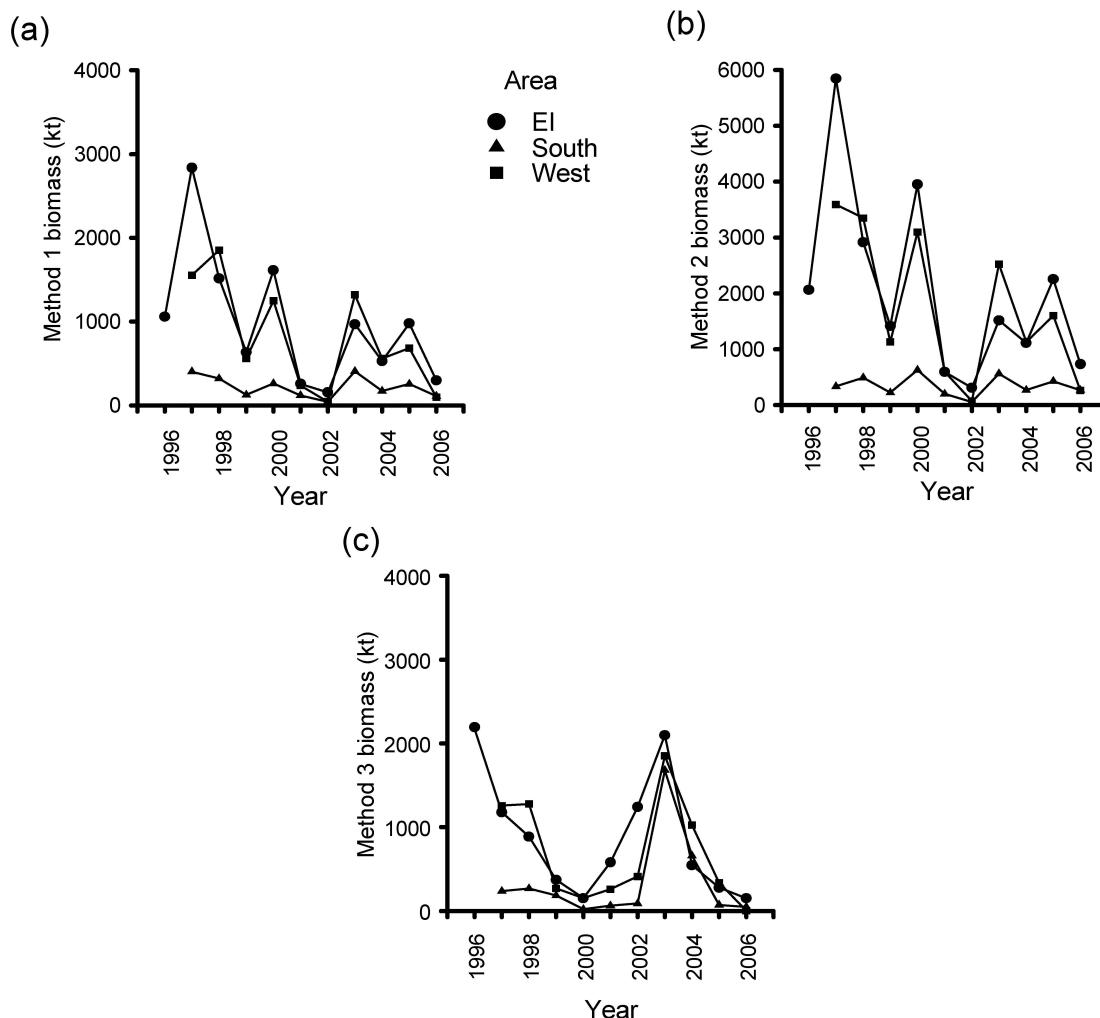
### Discussion

The variability in acoustically surveyed Antarctic krill biomass near the SSI between 1996 and 2006 was re-estimated using a validated physics-based model of TS, and an algorithm for acoustic identification of krill, derived from TS-model predictions (Method 3). This re-analysis resulted in biomass estimates similar in magnitude to previously published estimates used to examine krill population trends in the same area (Hewitt *et al.*, 2003). However, in contrast to the log-linear model for TS and the fixed  $\Delta S_v$  (Method 1) technique, the temporal pattern in the new estimates (Method 3) was similar to that derived from net-tow data, reflecting the sporadic nature of recruitment and cohort dominance, as described by Loeb *et al.* (1997).

The use of the variable  $\Delta S_v$  method, binned in 10-mm increments, to eliminate non-krill targets increased the CV of survey estimates by  $\sim 20\%$ , on average. This suggests an important trade-off between decreasing the  $\Delta S_v$  windows to eliminate non-krill targets and the perceived increased uncertainty in survey results. Yet, using the 10-mm binned increments still imposes some subjective decisions on the researcher. For example, during the first EI survey of 1997 (1997a), the size range of krill was 19–58 mm. The guidelines suggested by CCAMLR (2005) would include a window from 10 to 60 mm, and all that acoustic energy would be attributed to krill when no krill of those sizes were captured in the nets. Therefore, we truncated the length-bin range to 20–60 mm, eliminating a few krill that were just smaller than the window bins. Although it would be desirable to constrain the  $\Delta S_v$  species-discrimination algorithm to just those length frequencies observed from net tows, given the increase in the variability in biomass estimates using Method 3 compared with the fixed-window technique (Method 1), further constraining the  $\Delta S_v$  window may impact substantially on the utility of the survey estimates themselves. However, given the benefit of the better elimination of non-krill targets, it may be advisable to increase the number of transects in a survey to maintain acceptable levels of uncertainty, given the management goals.

The increase in CV arises from the patchiness of krill along individual transects. By constraining the  $\Delta S_v$  windows, more acoustic backscatter is considered acoustic noise and is not included in the biomass estimate, resulting in generally higher CVs when the survey biomass is calculated. In some cases, the survey CVs dropped with Method 3. A review of the acoustic data from those surveys did not show any predictable pattern, and the data suggest that these low CVs were not biased either to high or low recruitment years. In at least 1 year, the CV was  $< 1\%$  (Figure 5c; Appendix). Analysis of the acoustic data from that year showed that the low CV was associated with consistently low acoustic energy throughout the survey area, with few distinguishable patches, and low acoustic biomass.

Further, constraining the  $\Delta S_v$  windows to the lengths of krill solely captured within the nets requires a much better understanding of the selectivity of the net system to krill of different lengths.



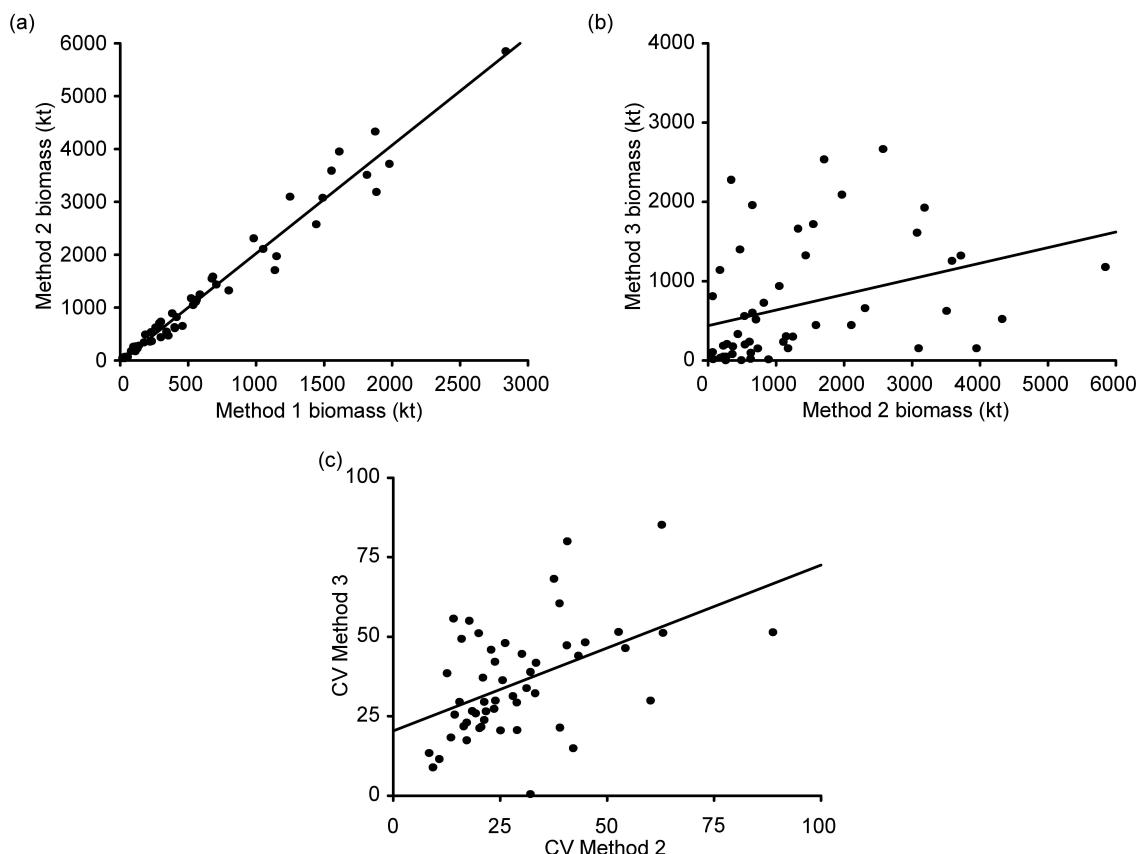
**Figure 4.** Time-series of the simple mean of “both legs” acoustic estimates of krill biomass between 1996 and 2006 for three areas around the SSI: EI, West, and South. (a) Method 1, fixed- $\Delta S_v$  technique for target identification (Watkins and Brierley, 2002), and the Greene TS model (Greene et al., 1991). (b) Method 2, fixed- $\Delta S_v$  technique and the simplified SDWBA TS model (Conti and Demer, 2006). (c) Method 3, variable- $\Delta S_v$  technique for target identification (see CCAMLR, 2005) and the simplified SDWBA TS model.

Our use of a 1.8-m<sup>2</sup> IKMT may undersample larger krill relative to their actual abundance, through net avoidance, and potentially truncate these length classes. There are few studies on the selectivity of nets for different lengths of krill. However, for our purposes, given that smaller krill will have a larger impact on acoustic estimates of biomass, we feel confident that any avoidance at larger sizes will not severely bias our estimates. Additionally, finely constraining the  $\Delta S_v$  windows requires a better understanding of the distributional pattern of krill lengths within catches, because it is common to find seeming “outliers”, individuals much smaller or larger than the bulk of the krill, in the area-averaged, krill length distributions. We have found little guidance within the literature as to how to include or exclude such “outliers”. Inclusion of small krill in these cases will greatly impact biomass estimates, given the non-linear nature of the TS relationship using the SDWBA method. A pragmatic approach to the issue was developed by CCAMLR (2007), whereby inclusion of krill to determine the  $\Delta S_v$  windows could be based on the distribution of 95% of the krill length frequencies estimated from a cumulative distribution function. We judged that our attempts to use this technique

eliminated too many krill in addition to the occasional outlier. However, when we used a distribution based on 99% of the krill lengths, the results of just two surveys changed appreciably. Therefore, except 2 years, we retained the suggested 10-mm window increments as outlined by CCAMLR (2005) and suggest that this is an important area for future examination.

Demer (2004) conducted a thorough study of the sources of random and systematic error in measurements and sampling during the 2000 Scotia Sea acoustic survey, and concluded that the overall CV accounting for measurement and sampling error was not significantly different from the sampling CV alone. He suggested that target identification and TS estimation could contribute more to significant sources of systematic error, and recognized that systematic error can result in apparent variability on various scales of time and space. Our re-analysis of 11 years of data supports this conclusion, and also reveals larger survey uncertainty than previously recognized.

The components of model-based uncertainty described by Demer (2004) were examined by Demer and Conti (2003a, b, 2005) and Conti and Demer (2006) to develop new methods to



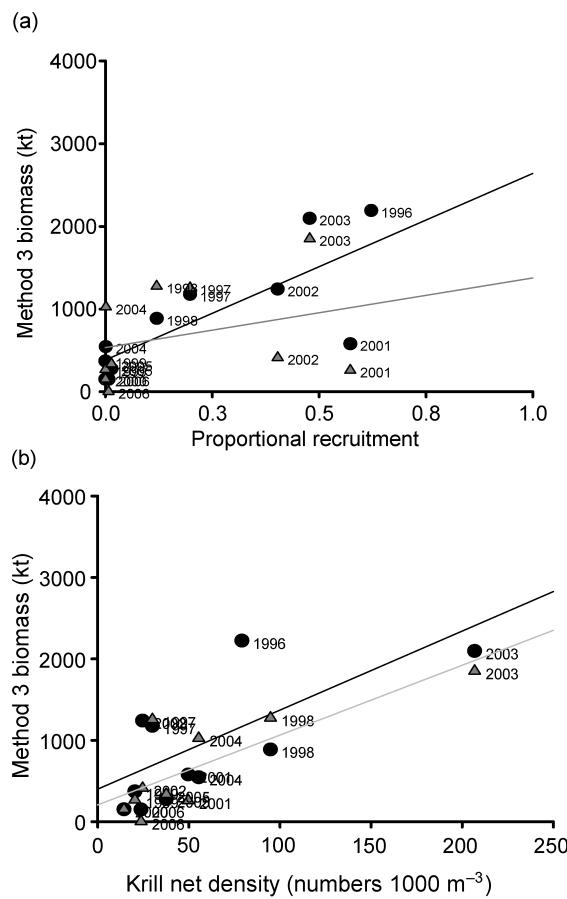
**Figure 5.** Correlations between krill biomass around the SSI estimated using (a) fixed- $\Delta S_v$  target identification technique and the Greene model vs. simplified SDWBA TS model (Method 1 vs. Method 2), (b) fixed- vs. variable- $\Delta S_v$  techniques and the simplified SDWBA TS model (Method 2 vs. Method 3), and (c) CVs of the biomass estimated using fixed- vs. variable- $\Delta S_v$  techniques and the simplified SDWBA TS model (Method 2 vs. Method 3).

reduce this uncertainty by using the simplified SDWBA. When we incorporated only the simplified SDWBA model for TS (Method 2), the acoustically based estimates of total biomass are approximately twice those calculated with the Greene model (Method 1). The CVs, dependent on the survey design, remained the same.

The time-series of acoustically estimated biomass derived from Methods 1 and 2 show interannual variations that are inconsistent with the life history of krill and the recruitment-driven density estimates in the time-series. However, using the variable  $\Delta S_v$  technique, TS predicted by the simplified SDWBA model, and area-specific krill length-pdfs (Method 3) produced time-series of acoustic estimates of total biomass similar in magnitude to estimates derived from Method 1, but which were correlated with krill density and proportional recruitment estimated from the net data. This is, in part, because the net data are used to “tune” the variable- $\Delta S_v$  technique and the method is therefore more efficient than the fixed- $\Delta S_v$  technique at filtering energy scattered from animals either smaller or larger than the krill. As noted above, this efficiency comes at the cost of increased average survey variability. More recently, Lawson *et al.* (2006) described an improved parameterization of Antarctic krill TS using the DWBA to model the scattering process. They suggested that in addition to describing more fully the shape and the orientation of krill, it would be useful to better understand the density contrast between krill and the water column, as well as sound-speed

variability. For retrospective analyses such as ours here, it is not possible to account for interannual variability in the density contrast of krill. However, CCAMLR (2005) analysed the sensitivity of estimates to these variables and showed that, relative to other sources of error, the sensitivity would be relatively minor, and would act simply to scale estimates of biomass when using the simplified SDWBA TS model.

Net-tow data include information on krill density and demography, and have been used to explore relationships between krill population dynamics and the environment (Siegel and Loeb, 1995; Loeb *et al.*, 1997; Siegel *et al.*, 2002). Despite the low sampling effort (ca. 100 stations per survey), and the high variances associated with the net-derived estimates of krill density, the krill demography documents episodic reproductive success, and maximal cohort biomass represented by individual krill 1 and 2 years old. Method 3 appears to provide a means for examining how total biomass varies among cohorts within the area, so may better describe the ontogenetic patterns of biomass around the South Shetlands. Here, during spring and summer, krill demonstrate a distinct separation of age/length categories, with young, small individuals, 1-year-old recruits from the previous years spawning, in shelf waters and Bransfield Strait (the South area), and large adults primarily in the offshore waters of Drake Passage (West area; Siegel, 1988). As a consequence, considering regional differences in krill size composition, Method 3



**Figure 6.** Correlations between (a) krill density and proportional recruitment, and (b) the krill biomass acoustically estimated using the variable- $\Delta S_v$  target identification technique and the simplified SDWBA TS model (Method 3) for the EI (black dots) and West areas (grey triangles), between 1996 and 2006.

accommodates demographically based distribution patterns. However, because acoustically estimated total biomass is dependent on the length-pdfs of krill collected in net tows, net-tow data are increasingly imprecise for smaller areas. Hence, care is required when examining variability in biomass in areas of differing size.

Currently the total allowable catch for the krill fishery in the Southern Ocean is derived from an age-based model of krill population dynamics in which recruitment is modelled as a random process mimicking the recruitment-variability-driven dynamics observed in net-tow and acoustic data (Hewitt and Linen Low, 2000). Survey biomass and its CV are used to develop catch-allocation schemes under two conditions: (i) that the probability that population biomass will fall below 20% of  $B_0$  is 10%, and (ii) that the median population level is 75% or greater to protect predators dependent on krill (Hewitt and Linen Low, 2000). Simulations are run for 20 years, and harvest rates then set as a percentage of this  $B_0$ , i.e. directly related to estimates of biomass and the CV. Given the increase in variability in Method 3, and the essentially similar mean biomass estimated from Method 1, it seems likely that future allocations will be more conservative than at present, based in part on awareness of the true uncertainty in biomass estimates.

A number of studies has documented the quasi-periodic fluctuations of krill abundance in the Scotia Sea using net data (Brierley *et al.*, 1999; Reid *et al.*, 2002; Siegel *et al.*, 2003). Good accord was found between abundance off the western Antarctic Peninsula and around the South Shetlands (Siegel *et al.*, 2003), and between the South Shetlands and South Georgia (Brierley *et al.*, 1999; Reid *et al.*, 2002). Always, the fluctuations were linked to cohort succession that exhibited a period of  $\sim 4\text{--}5$  years. Hewitt *et al.* (2003) analysed the acoustic data from the South Shetlands and explained 75% of the variability in their time-series (1992–2002) when an 8-year cycle was fitted to the data. However, the new time-series of krill biomass, acoustically derived using the variable- $\Delta S_v$  and TS predicted by the simplified SDWBA model and krill length-pdfs for each area, suggest a different scenario: the largest biomasses, mostly 1-year-olds, were in 1996 and in 2003, rather than the previously calculated peak in 1998 and a broader 3-year high from 2001 to 2003. Such differences could have great ramifications on studies that hypothesize links between krill biomass and the reproductive success of land-based predators.

The current  $B_0$  survey CV and allocation scheme (CCAMLR, 2007), which uses the SDWBA model and the variable species-discrimination model, still only encompasses variability associated with a single survey, so does not represent the population variability. From a perspective of the population dynamics, the revised estimates of biomass calculated with Method 3, which are similar to the biological recruitment patterns and correlated with net-based density estimates, will be useful in understanding population variability over time. Moreover, this temporal variability may be useful in understanding the relationship between krill and their land-based predators. A major component of the current management strategy is to ensure that predator reproductive success is not compromised by overharvesting krill, especially near the nesting and pupping areas of penguins and seals (Hewitt *et al.*, 2004b). Therefore, the new time-series of abundance provides managers with information regarding trends in biomass that may better correlate with the reproductive success of predators.

Hill *et al.* (2007) argued the importance of examining the differences in competing models to ascertain whether management outcomes would differ based on their underlying structures (e.g. Method 2 vs. Method 3). Given the recent improvement in the ability to model the TS of krill, especially to identify it with more certainty, Method 3 has potentially reduced the uncertainty for acoustically estimating krill biomass because the model is physics-based. The time-series of biomass better reflects the natural population variability and the ontogenetic patterns of krill derived from net tows, and, more importantly, reflects the biology of this recruitment-dominated animal, despite a larger survey uncertainty than previously recognized. The increased variability associated with the elimination of non-krill scatterers using Method 3 suggests that future surveys will either need to increase the number of transects within areas to better constrain the survey variability, or devise mechanisms to mitigate this variability. Given the current management strategy, which relies on acoustic estimates of biomass and its variability to allocate catch, failure to account properly for the increase in variability is likely to result in a more precautionary yield. Additionally, CCAMLR has recently started to develop a strategy to allocate the allowable catch to smaller management units to protect land-based predators. In future, therefore, it will be important to consider whether Method 3

will better discern the probability that fishing, rather than natural variability, might be responsible for reproductive failures of land-based predators such as fur seals and penguins than Method 2, a critical management goal for CCAMLR (Hewitt *et al.*, 2004b; CCAMLR, 2006; Hill *et al.*, 2007).

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## Appendix

**Table A1.** Acoustics-based biomass estimates (kt) of Antarctic krill in the El, West and South areas of the South Shetland Islands region between 1996 and 2006, using the fixed- $\Delta S_v$  technique for target identification and the Greene TS model (Greene *et al.*, 1991), the fixed- $\Delta S_v$  technique and the simplified SDWBA TS model (Conti and Demer, 2006) and the variable- $\Delta S_v$  technique for target identification (see CCAMLR, 2005) and the simplified SDWBA TS model.

| Area     | Year | Greene TS model fixed- $\Delta S_v$ identification | Simplified SDWBA fixed- $\Delta S_v$ identification | Greene/SDWBACV | Simplified SDWBA variable- $\Delta S_v$ identification | Variable CV |
|----------|------|--|---|----------------|--|-------------|
| Elephant | 1996 | 1 443 626  | 2 576 825   | 28.98          | 2 665 790  | 28.50       |
| Island   | 1996 | 675 501  | 1 548 478   | 28.89          | 1 719 927  | 29.26       |
|          | 1997 | 2 838 128  | 5 847 864   | 21.29          | 1 178 323  | 23.78       |
|          | 1998 | 1 981 888  | 3 720 272   | 14.44          | 1 323 676  | 25.51       |
|          | 1998 | 1 052 836  | 2 109 155   | 15.47          | 445 793  | 29.45       |
|          | 1999 | 587 060  | 1 247 306   | 40.63          | 299 659  | 47.34       |
|          | 1999 | 682 173  | 1 587 910   | 37.58          | 445 793  | 68.15       |
|          | 2000 | 1 612 995  | 3 951 729   | 25.62          | 152 987  | 36.26       |
|          | 2001 | 227 839  | 536 127   | 20.61          | 559 986  | 21.56       |
|          | 2001 | 287 855  | 652 213   | 10.83          | 601 986  | 11.45       |
|          | 2002 | 175 442  | 339 427   | 42.05          | 2 277 405  | 14.90       |
|          | 2002 | 136 339  | 279 381   | 21.71          | 207 622  | 26.54       |
|          | 2003 | 1 138 960  | 1 708 077   | 8.44           | 2 535 116  | 13.39       |
|          | 2003 | 799 527  | 1 323 926   | 20.23          | 1 660 834  | 21.17       |
|          | 2004 | 536 953  | 1 048 387   | 17.18          | 939 275  | 17.38       |
|          | 2004 | 522 161  | 1 176 701   | 23.76          | 153 923  | 42.11       |
|          | 2005 | 1 877 496  | 4 329 478   | 17.81          | 523 369  | 54.98       |
|          | 2005 | 81 537   | 179 708   | 20.96          | 32 931   | 37.07       |
|          | 2006 | 299 511  | 732 655   | 32.09          | 151 706  | 38.94       |
| West     | 1997 | 1 555 264  | 3 589 875   | 28.04          | 1 256 851  | 31.31       |
|          | 1998 | 1 886 523  | 3 187 024   | 19.24          | 1 926 825  | 25.86       |
|          | 1998 | 1 816 411  | 3 510 690   | 23.57          | 625 096  | 27.25       |
|          | 1999 | 563 308  | 1 148 670   | 31.22          | 303 604  | 33.77       |
|          | 1999 | 556 242  | 1 108 069   | 33.35          | 235 034  | 41.81       |
|          | 2000 | 1 250 538  | 3 097 539   | 33.15          | 154 004  | 32.22       |
|          | 2001 | 185 596  | 489 103   | 19.95          | 4 318  | 51.11       |
|          | 2001 | 288 840  | 705 097   | 38.92          | 516 310  | 60.50       |
|          | 2002 | 33 274   | 67 785  | 30.10          | 809 628  | 44.63       |
|          | 2002 | 53 581   | 75 122  | 54.25          | 15 661   | 46.36       |
|          | 2003 | 1 151 374  | 1 970 578   | 16.5           | 2 091 244  | 21.79       |
|          | 2003 | 1 490 733  | 3 076 555   | 21.24          | 1 611 244  | 29.54       |
|          | 2004 | 707 516  | 1 435 675   | 9.26           | 1 324 195  | 8.89        |
|          | 2004 | 415 377  | 820 321   | 43.25          | 727 087  | 44.01       |
|          | 2005 | 982 492  | 2 310 577   | 18.46          | 659 241  | 26.56       |
|          | 2005 | 383 362  | 890 554   | 62.81          | 14 204   | 85.16       |
|          | 2006 | 97 411   | 260 118   | 22.85          | 3 143  | 45.85       |
| South    | 1997 | 402 556  | 608 592   | 69.19          | 236 069  | 51.22       |
|          | 1998 | 299 560  | 437 716   | 17.22          | 332 982  | 22.96       |

Continued

**Table A1.** *Continued*

| <b>Area</b> | <b>Year</b> | <b>Greene TS model fixed-<math>\Delta S_v</math> identification</b> | <b>Simplified SDWBA fixed-<math>\Delta S_v</math> identification</b> | <b>Greene/SDWBACV</b> | <b>Simplified SDWBA variable-<math>\Delta S_v</math> identification</b> | <b>Variable CV</b> |
|-------------|-------------|---|--|-----------------------|---|--------------------|
|             | 1998        | 341 224   | 543 675  | 12.63                 | 200 531   | 38.48              |
|             | 1999        | 126 008   | 223 311  | 13.47                 | 186 348   | 18.26              |
|             | 2000        | 261 593   | 625 916  | 32.11                 | 20 328  | 0.51               |
|             | 2001        | 220 264   | 355 407  | 60.24                 | 79 711  | 29.93              |
|             | 2001        | 17 499  | 42 859   | 52.70                 | 45 471  | 51.49              |
|             | 2002        | 54 547  | 66 560   | 44.88                 | 104 858   | 48.16              |
|             | 2002        | 33 850  | 43 798   | 40.67                 | 72 647  | 79.94              |
|             | 2003        | 353 842   | 469 794  | 23.90                 | 1 399 854   | 29.89              |
|             | 2003        | 458 589   | 651 726  | 25.06                 | 1 958 945   | 20.45              |
|             | 2004        | 232 704   | 364 759  | 26.21                 | 176 769   | 47.97              |
|             | 2004        | 112 279   | 173 496  | 88.82                 | 1 140 570   | 51.43              |
|             | 2005        | 400 944   | 628 472  | 14.08                 | 96 142  | 55.66              |
|             | 2005        | 110 782   | 223 399  | 39.01                 | 48 247  | 21.39              |
|             | 2006        | 111 932   | 265 856  | 18.95                 | 47 689  | 49.34              |

CVs of the Greene TS model and Simplified SDWBA TS model with fixed- $\Delta S_v$  target identification are the same.

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